

Larval settlement and recruitment of a brackish water clam, *Corbicula japonica*, in the Kiso estuaries, central Japan

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Abstract: Population dynamics of the brackish water clam *Corbicula japonica* were examined in the Kiso estuaries (the Ibi-Nagara Estuary and the Kiso Estuary), central Japan, during the process of larval recruitment. Based on temporal variation in densities (sampling every 2 weeks for planktonic larvae, new settlers, and small individuals, sampling every month for large and commercially important individuals) from May 2001 to April 2004, we conclude that densities of large and of commercially important individuals were determined not by larval supply but by benthic processes. Density-dependent processes were detected between densities of new settlers and recruits. These processes, however, were detected for spring-summer cohorts, but not for autumn-winter cohorts. Spatial distributions of each cohort were almost the same within the Ibi-Nagara Estuary and within the Kiso Estuary, although cohorts were collected mainly in the middle to upper regions of the Ibi-Nagara Estuary but were collected in the upper region of the Kiso Estuary. A shift in an ontogenetic habitat within each cohort was detected in the Ibi-Nagara Estuary but not in the Kiso Estuary: New settlers and small individuals were collected in the upper region while large and commercially important individuals were collected in the middle region. The shift may be explained by tidal migration using byssal threads or by site-specific differences in mortality, although it was not clear why the shift was detected in the Ibi-Nagara Estuary but not in the Kiso Estuary.

Key words: population dynamics, density-dependent processes, commercially important species

The brackish water clam *Corbicula japonica* (Prime, 1864) is endemic to eastern Asia (Sakai *et al.* 1994, Harada and Nishino 1995). The clam is commonly found in estuarine waters throughout Japan except for the Ryukyu Archipelago, southern Japan, which geographically belongs to the Subtropical/Tropical Zone. The species is a target for clam fisheries in Japan, especially in the Kiso estuaries (the Ibi-Nagara and the Kiso Rivers), central Japan (see Nakamura 2000). Despite several regulations imposed to manage fisheries of *Corbicula* in Japan, the total annual catch yields of *Corbicula* species (of which approximately 99% is *C. japonica*) have decreased drastically over the last two or three decades (Mizuno *et al.* 2005), probably through the progress of eutrophication in the estuarine and coastal waters of Japan. This is true for the yields in the Kiso estuaries as well as in other areas of Japan. Traditionally in Japan, the larger hard shell clam *Meretrix lusoria* (Röding, 1798) has been commercially more important than *C. japonica*. A drastic decrease in the yield of *M. lusoria* in the Kiso estuaries occurred in the late 1970s, when the yield of *C. japonica* abruptly increased (Mizuno *et al.* 2005). This resulted in a much greater fishing effort for *C. japonica*. However, the yields of *C. japonica* in the Kiso estuaries has drastically decreased since early 1980s despite several regulations imposed on the fishery. The causes or mechanisms by which the drastic decrease in the yield of *C. japonica* in the Kiso estuaries, as well as in the other areas of Japan, may be driven are not well understood (see Nakamura 2000).

Recent studies on marine benthic invertebrates have emphasized the role of larval recruitment in the population dynamics of intertidal and subtidal organisms that have complex life cycles (those that include planktonic and benthic phases) (*e.g.*, Roughgarden *et al.* 1988, Underwood and Keough 2001), although few studies have been made in the marine environment, probably due to difficulties in identifying planktonic larvae (*e.g.*, Sakai and Sekiguchi 1992), in examining the coupling of larval transport and dispersal with oceanographic conditions (*e.g.*, Roughgarden *et al.* 1988), and in discovering larval settlement processes (*e.g.*, Connell 1985, Gaines and Roughgarden 1985, Gaines *et al.* 1985). This situation has been true also for bivalves, including the clams that are commercially important in Japan (see Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, 2001b). Unfortunately, there is not sufficient data on larval recruitment of *Corbicula japonica*, in contrast to the clam *Ruditapes philippinarum* (Adams and Reeve, 1850), which dominates Japanese tidal flats (Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, 2001b).

Tolerance to varying salinity by planktonic larvae and benthic stages of *Corbicula japonica* was examined in the laboratory by Tanaka (1984a, b) and Saito *et al.* (2002). Tidal transport of the larvae was investigated in relation to the salinity distribution in estuarine waters in the Kiso estuaries by Sekiguchi *et al.* (1991) and in the laboratory by Kuwabara and Saito (2003). In Lake Shinji where *C. japonica* is the most important target species for clam fisheries, growth of

benthic stages of the clam was examined by Takada *et al.* (2001) and Oshima *et al.* (2004). Takada *et al.* (2001) also studied the seasonal abundance of spat of the clam, estimating the season of larval settlement. However, larval recruitment of the clam has not been studied. Nanbu *et al.* (2005) examined the spatio-temporal variations in densities of different life stages (planktonic larvae, new settlers, and small, large and commercially important individuals) of the clam in the Kiso estuaries, central Japan, to understand larval recruitment, by which benthic populations may be generated and maintained in the estuaries. In contrast to the other common and abundant bivalves (*Ruditapes philippinarum*, *Musculista senhousia* [Benson, 1842], and *Macra veneriformis* Deshayes in Reeve, 1854), of which all life stages were detected around the river mouths, *C. japonica* showed a marked ontogenetic habitat shift in the Ibi-Nagara Estuary, but not in the Kiso Estuary. The primary habitat for new settlers and small individuals and of large and commercially important individuals of *C. japonica* was located in the upper and middle regions of the Ibi-Nagara Estuary, while the benthic stages were primarily found in the upper region of the Kiso Estuary. However, it is not clear whether the ontogenetic habitat shift is generated by migration during benthic stages or by differences in site-specific mortality of new recruits.

To understand the population dynamics of *Corbicula japonica* in the Kiso estuaries, we examined which life stage may determine the strength of catch yields (or population size) of the clam, and whether the ontogenetic habitat shift of the clam may be generated by migration during benthic stages or by differences in site-specific mortality, using the cohort separation based on three years of data (from May 2001 until April 2004) collected in the Kiso estuaries. Nanbu *et al.* (2005) examined spatio-temporal distributions of densities of each life stage of the clam, using the first two years of data from the present study.

METHODS

Study area

The Kiso Rivers (the Ibi, Nagara, and Kiso Rivers), three of the largest rivers in Japan, flow into Ise Bay on the Pacific coast of central Japan (Fig. 1). The Ibi and the Nagara Rivers join at their lower regions where both rivers are united into the Ibi-Nagara River. The Nagara River, however, has recently been closed at a point 5 km upstream by the Nagara Dam (Fig. 1). The Kiso estuaries (the Ibi-Nagara and the Kiso Estuaries), defined as the areas where bottom water has a detectable salinity of 1.0 psu, are 2-10 m in depth and have a maximal tidal range of 3 m, reaching 30 km upstream for the Ibi River and 26 km upstream (where there is a dam) for the Kiso Estuary (Japan Society of Oceanography 1985).

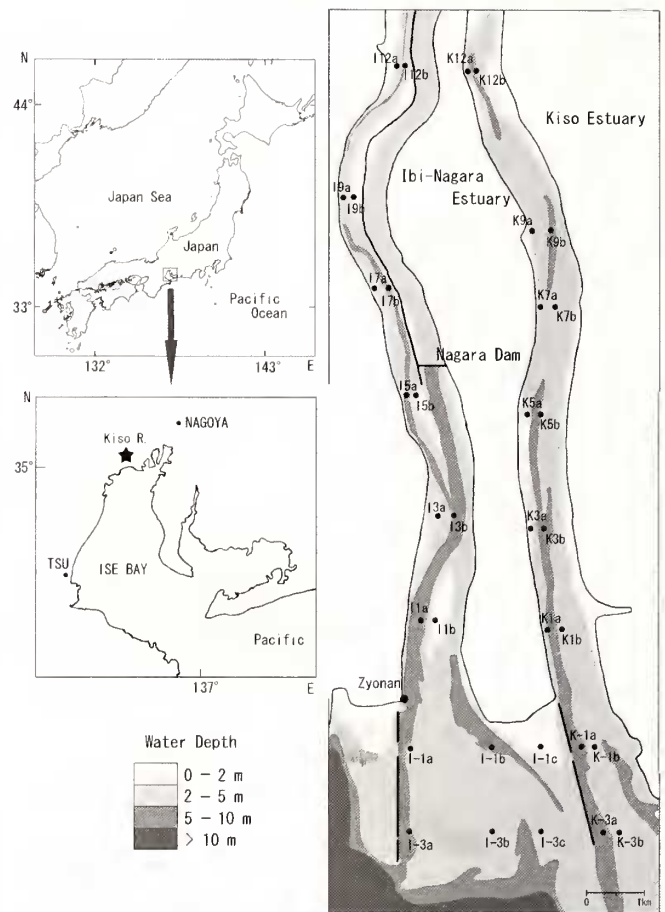


Figure 1. Study area and location of sampling stations. Solid circles, sampling stations with 2 or 3 sites (e.g., I-1a, I-1b) within each sampling station; bold solid lines seaward from the estuary mouth, protection bars against the tide.

Environmental characteristics

For the last decade, the Kiso River Management Office of the Ministry of Transport and Infrastructure has continuously monitored water temperature and salinity every hour in water 0.5 m above the bottom at a site 0.5 km upstream in the Ibi-Nagara Estuary (Zyonan, see Fig. 1 for location). To examine environmental characteristics of the Kiso estuaries, we used averages over 24 h of these environmental data obtained from that office (Fig. 2A). Although we have no similar data available for the Kiso Estuary, environmental conditions are similar at the mouths of these estuaries (Mizuno *et al.* 2005).

According to Mizuno *et al.* (2005), the silt-clay fraction of sediments in the Kiso estuaries is usually less than 5.0% in dry weight, being much higher at the mouths and downstream areas of these estuaries, and lower in the upstream areas. Accordingly, bottom sediments are sandy 5 km or

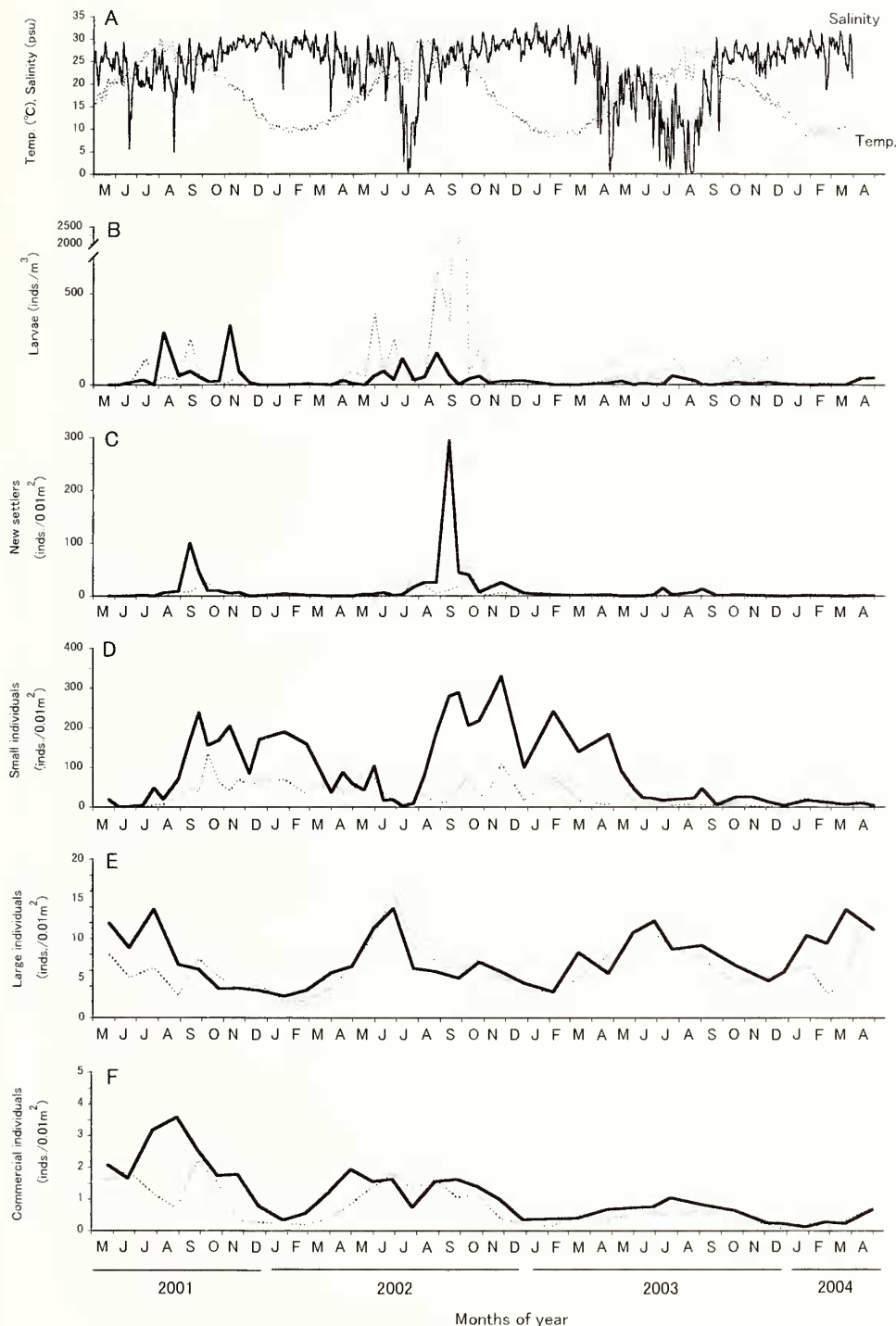


Figure 2. A, Water temperature and salinity in the Kiso estuaries, central Japan. B-F, Variation in average densities of different life stages (planktonic larvae, new settlers, small individuals, large individuals, and commercially important individuals) in the Kiso estuaries, central Japan. Solid lines, the Ibi-Nagara Estuary; dotted lines, the Kiso Estuary.

more upstream of these estuaries, although an extraordinarily high percentage (50% or more) of the silt-clay fraction occurs in the area closest to the Nagara Dam. Muddy sediment was common in troughs, so that the silt-clay fraction was very different between troughs and ridges, even at the same distance from the mouths of the estuaries.

Sampling procedures

Sampling was undertaken in the Kiso estuaries from May 2001 until April 2004. The study area, environmental characteristics, sampling procedures, and data processing were described in detail in Nanbu *et al.* (2005).

Planktonic larvae of *Corbicula japonica* were obtained at

stations located 1 km seaward of each river mouth (I-1a and I-1b in the Ibi-Nagara Estuary, K-1a and K-1b in the Kiso Estuary) (Fig. 1) using a vertical haul of plankton nets (22 cm in diameter, 133 μm mesh openings) from the bottom to the surface every 2 weeks (except for January to March 2002). Larval density was indicated as individuals/ m^3 . Bivalve larvae were identified to species using a compound microscope according to Sakai and Sekiguchi (1992) and Kimura *et al.* (2004).

For sampling benthic stages of *Corbicula japonica*, 8 stations (I-3, I-1, I1, I2, I5, I7, I9, and I12 for the Ibi-Nagara Estuary, K-3, K-1, K1, K3, K5, K7, K9, and K12 for the Kiso Estuary) were located every 2 or 3 km up to 12 km upstream from the river mouth in each estuary and also 2 or 3 sites 1 km and 3 km downstream/seaward from the mouth, respectively (Fig. 1). Samples were collected at 2 or 3 sites with different depths within each sampling station area. To sample new settlers and small individuals, one sediment sample was collected with a core sampler (3.1 cm in diameter, 1.0 cm depth) from the surface layer of bottom sediments which were obtained at each site within each station using a Smith-McIntyre grab. For sampling large and commercially important individuals, one sediment sample was obtained at each site within each station using a Smith-McIntyre grab. New settlers and small individuals of the clam were collected every 2 weeks while large and commercially important individuals were collected every month. Identification of new settlers and small individuals of *C. japonica* was done following Sakai and Sekiguchi (1992) and Kimura *et al.* (2004). Density of the benthic stages of the clam was indicated as individuals/ 0.01m^2 .

The life stages of *Corbicula japonica* were defined as in Nanbu *et al.* (2005): "Planktonic larvae" were D-shaped larvae (i.e. early-stage veligers); "new settlers" were individuals with shell lengths less than 300 μm ; "small individuals" were ones with shell lengths 0.3 mm or more but less than 1.0 mm; "large individuals" were ones with shell lengths of 1.0 mm or more but less than 12.0 mm; "commercial individuals" were ones with shell lengths of 12.0 mm or more. These definitions are the same as those used to describe bivalves that are common in Japanese tidal flats (e.g., *Ruditapes philippinarum*) by Sekiguchi and his co-workers (e.g., Miyawaki and Sekiguchi 1999, 2000, Ishii *et al.* 2001a, b, Nanbu *et al.* 2005) except for planktonic larvae. We defined "successful recruitment" as new settlers and small individuals that reached average shell lengths of 1.0 mm or more for each cohort.

Data analysis

Sediment samples were collected at 2 or 3 sites within each station. The density of each life stage of *C. japonica* was not significantly different between sites within each station

(t-test, $p > 0.05$). We used average densities of each life stage. Based on these averages for the period from May 2001 to April 2004, we examined the differences in density of each life stage between the two estuaries and between sampling year for each estuary, using Mann-Whitney's U-test (significance level, $\alpha = 0.05$) and Kruskal-Wallis's H-test (significance level, $\alpha = 0.05$), respectively. We used Bonferroni's method ($\alpha' = 0.05$) when significant differences in density were detected between sampling years.

To separate each cohort, the shell lengths for the two groups (new settlers/small individual group, large/commercial individual group) were compiled for all stations of each estuary. However, it was difficult to separate each cohort for commercial individuals due to their small numbers. Based on these data, cohorts within each group were identified by the method of Akamine (1985), who separated polymodal length distribution into two or more normal distributions. The growth curve of each cohort was estimated based on temporal change of the mean shell length of each normal distribution.

Estimation of densities of new settlers and recruits of *Corbicula japonica*

To examine the relationships between the densities of new settlers and recruits (i.e., large individuals) of the clam, using the data for cohorts that were successful in recruitment, we estimated densities of new settlers and recruits, respectively, as follows: Based on the growth curve of each successful cohort, we determined the day when average shell lengths of new settlers reached 1.0 mm. Then, assuming larval settlement day as day 0 when new settlers of each successful cohort were first collected, we fitted a regression line to the temporal change of each cohort density using a graph in which the X-axis was days after larval settlement of each successful cohort and the Y-axis was the log-transformed density of each successful cohort. Using the density data estimated for successful cohorts with a significant ($p < 0.05$) regression line, we examined the relationships between the densities of new settlers and recruits (i.e., based on the data for each estuary and then for each estuary according to season), and then the relationships between the density of new settlers and the ratio of their densities (recruits/new settlers) (i.e., based on the data for each estuary and then for each estuary according to season).

RESULTS

Variation in densities of different life stages of *Corbicula japonica*

The densities of planktonic larvae peaked primarily in May to December every year (Fig. 2B). There was no sig-

nificant difference in larval density between the Ibi-Nagara and the Kiso Estuaries nor between sampling years for each estuary (Table 1). As seen in Fig. 2B, however, larval density in 2003 appeared to be lower than in the other years, probably due to more days with less than 10 psu in 2003 than in the other years, because salinity preferred by spawning of the clam is in the range of 9.35-21.82 psu (Asahina 1941).

Water temperature reached about 30°C in summer and decreased below 10°C in winter (Fig. 2A). On the other hand, although tending to become lower in summer and higher in winter, salinity did not indicate such a clear seasonal change but always showed irregular variations (about 15-32 psu) and occasionally marked lowering (down to <1 psu, corresponding to low larval density) owing to freshwater discharge through high rainfall in early summer. Larval densities were low or larvae were completely absent from the water column usually from December to the following April, when the water temperature decreased to below 15°C. According to laboratory rearing experiments (Kimura *et al.* 2004), larvae of the clam reared at 15°C or lower failed to settle and recruit. The larvae from earlier and later portions of a much longer period spawning of the clam every year may not contribute to generating cohorts of new settlers.

The densities of new settlers peaked primarily in July to

August every year (Fig. 2C). There was no significant difference in density between the two estuaries (except for 2003) nor between sampling years for each estuary (Table 1), although the density in 2003 appeared to be lower than in the other years, possibly due to a lower larval density in 2003.

Higher densities of small individuals were found for a longer period than new settlers, occurring from August to the following April (Fig. 2D), although the density appeared to be much lower in 2003 than in the other years. In each year, density of small individuals was significantly higher in the Ibi-Nagara Estuary than in the Kiso Estuary (Table 1). The Kiso Estuary had a higher density in 2002; otherwise there was no significant difference in the density of small individuals between sampling year for each estuary (Table 1).

Variation in densities of large individuals was very similar between the two estuaries (Fig. 2E). There was no significant difference in density between these estuaries and also between sampling year for each estuary (Table 1). As seen in Fig. 2E, however, the density of large individuals appeared to be higher in 2003 than in the other years, in contrast to larvae and new settlers/small individuals (Table 1).

The density of commercially important individuals was

Table 1. Differences in densities of different life stages of *Corbicula japonica* between the Ibi-Nagara and the Kiso estuaries and between sampling years for each estuary.

2001	Ibi-Nagara	Kiso	Ibi-Nagara	Sampling year
Larvae	—	—	Larvae	2002 = 2001 = 2003 [] = []
New settlers	—	—	New settlers	2002 = 2001 = 2003 [] = []
Small individuals	○	×	Small individuals	2002 = 2001 = 2003 [] = []
Large individuals	—	—	Large individuals	2003 = 2001 = 2002 [] = []
Commercial individuals	○	×	Commercial individuals	2001 > 2002 > 2003 [] > []
2002	Ibi-Nagara	Kiso	Kiso	Sampling year
Larvae	—	—	Larvae	2002 = 2001 = 2003 [] = []
New settlers	—	—	New settlers	2002 = 2001 = 2003 [] = []
Small individuals	○	×	Small individuals	2002 = 2001 = 2003 [] > []
Large individuals	—	—	Large individuals	2003 = 2002 = 2001 [] = []
Commercial individuals	—	—	Commercial individuals	2001 > 2002 > 2003 [] = []
2003	Ibi-Nagara	Kiso		
Larvae	—	—		
New settlers	○	×		
Small individuals	○	×		
Large individuals	—	—		
Commercial individuals	—	—		

Mann-Whitney's U-test (significance level, $\alpha = 0.05$).

○: significant difference with higher density.

×: significant difference with lower density.

—: no significant difference.

Kruskal-Wallis' H-test (significance level, $\alpha = 0.05$).

>: significant difference.

=: no significant difference.

Multiple comparison ($\alpha' = 0.05$; Bonferroni's method).

significantly lower in 2003 than in the other years (Table 1) and their density appeared to decline from 2001 to 2004 (Fig. 2F).

Cohort separation of *Corbicula japonica*

In the Ibi-Nagara Estuary, 21 cohorts of new settlers and small individuals and 16 cohorts of large individuals were identified (Fig. 3B). Of these cohorts, 7 were found to settle

and to succeed in recruitment through the three-year investigation. Larval settlement for 2 cohorts (i, ii) occurred in August to September 2001. For 4 cohorts (iii-vi), the larval settlement season in 2002 varied depending on cohort: Cohorts iii, iv, and v settled in January, May to June, and September, respectively. Larval settlement for the remaining cohort occurred in April of 2003. Of these 7 cohorts, significant regression lines were fitted to the temporal change

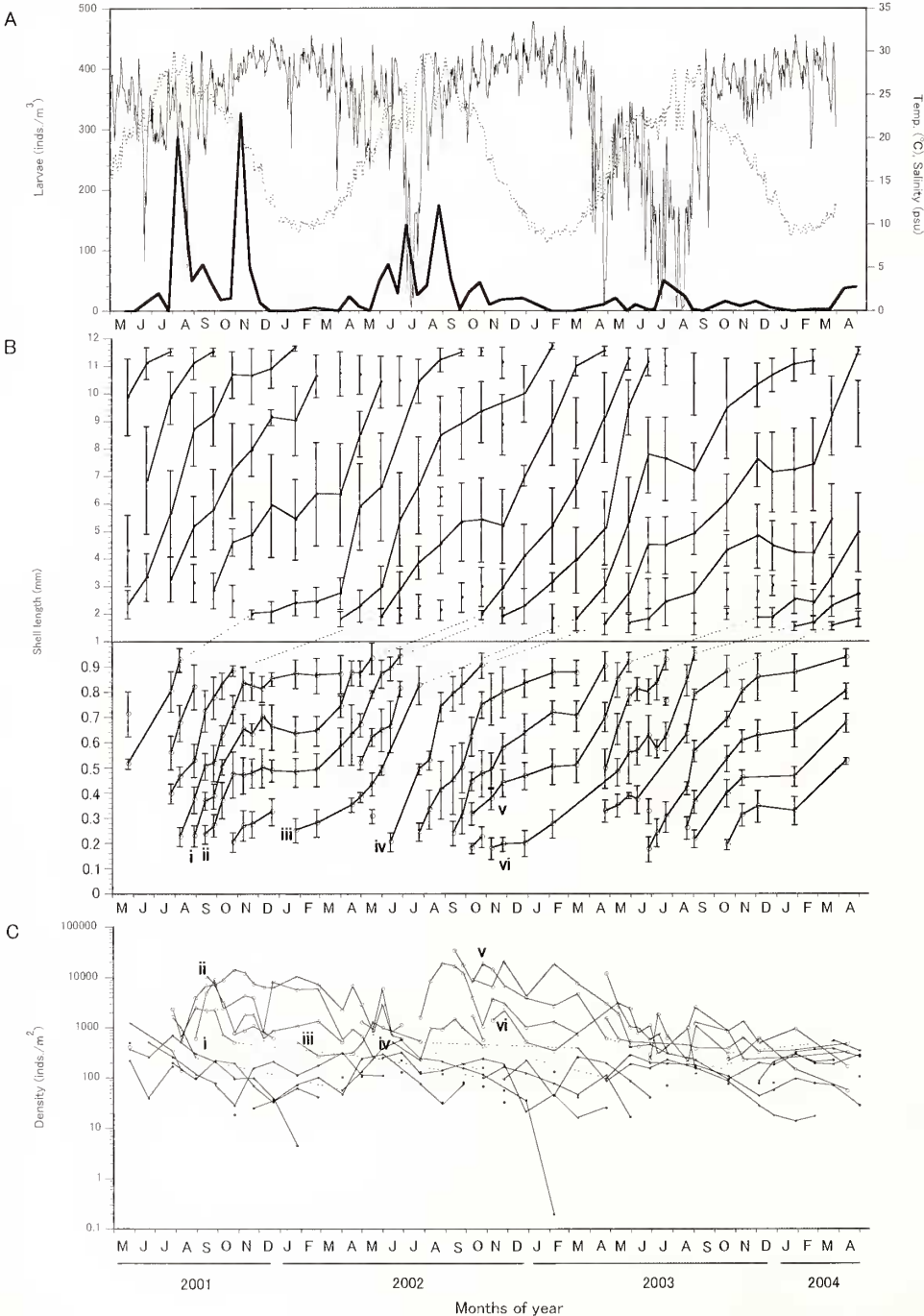


Figure 3. Cohorts of benthic stages of *Corbicula japonica* in the Ibi-Nagara Estuary, central Japan. A, Bold solid lines, larval density; thin solid lines, salinity; dotted lines, water temperature. B, i-vi, cohorts successful in recruitment; solid or open circles with vertical lines, averages of shell lengths and standard error; horizontal solid line, shell length 1.0 mm, which we defined as the size for successful recruitment. C, i-vi, cohorts same as in B.

of density from larval settlement to recruitment for 6 cohorts (cohort i-vi) (Fig. 3C). These cohorts (except cohort iii) appeared to settle in August to November.

In the Kiso Estuary, 12 cohorts of new settlers and small individuals and 13 cohorts of large individuals were identified (Fig. 4B). Of these cohorts, 7 were detected to settle and to succeed in recruitment through the three-year investigation. Larval settlement for cohorts 1 and 2 occurred in

August to September 2001. For 3 cohorts (3-5), larval settlement occurred in July to September 2002. Larval settlement for the remaining 2 cohorts occurred in December 2002 and in July 2003, respectively. Significant regression lines were fitted to the temporal change of density from larval settlement to recruitment for 5 cohorts (1-5) (Fig. 4C). These cohorts appeared to settle in July to September.

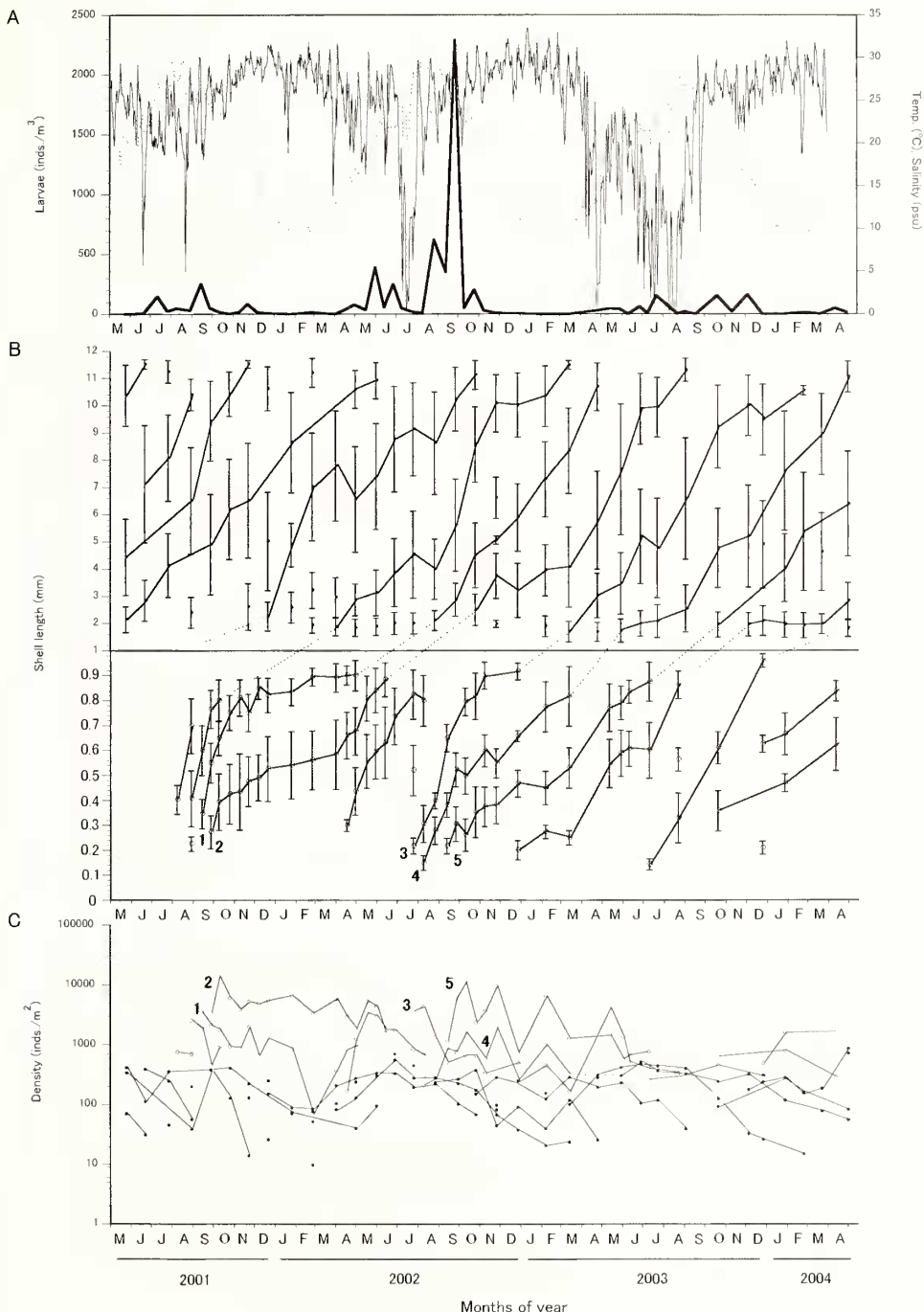


Figure 4. Cohorts of benthic stages of *Corbicula japonica* in the Kiso Estuary, central Japan. A, Bold solid lines, larval density; thin solid lines, salinity; dotted lines, water temperature. B, 1-5, cohorts successful in recruitment; solid or open circles with vertical lines, averages of shell lengths and standard error; horizontal solid line, shell length 1.0 mm, which we defined as the size for successful recruitment. C, 1-5, cohorts same as in B.

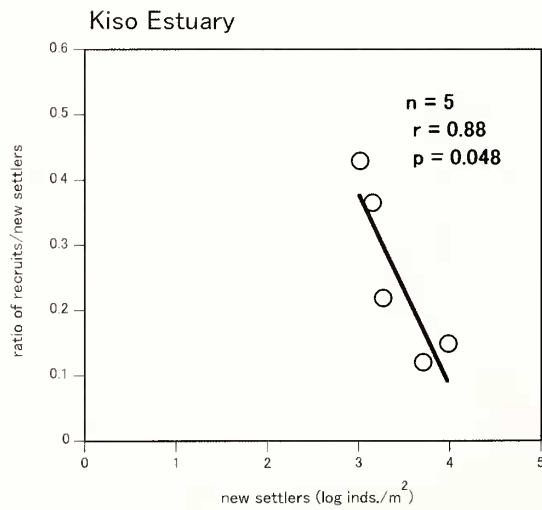
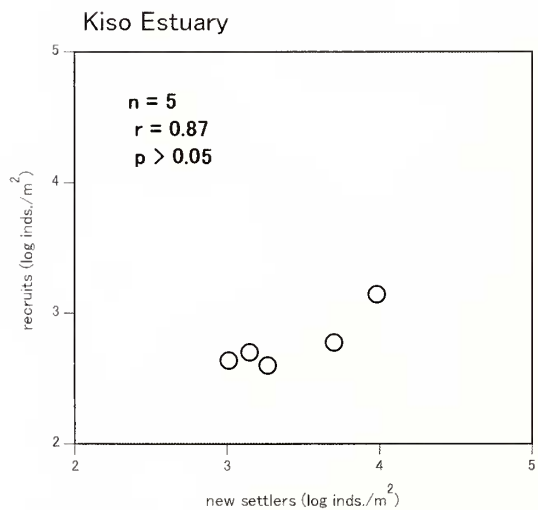
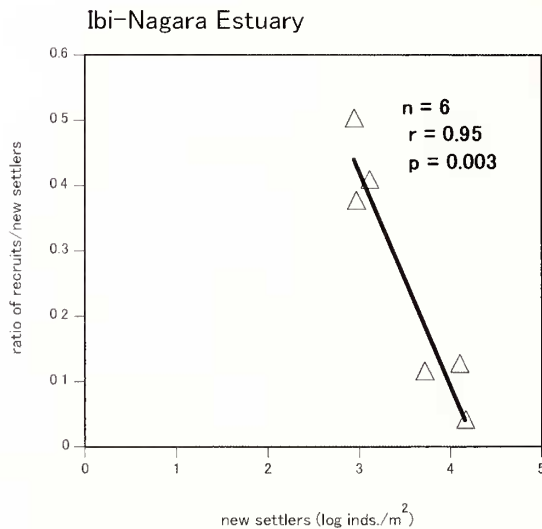
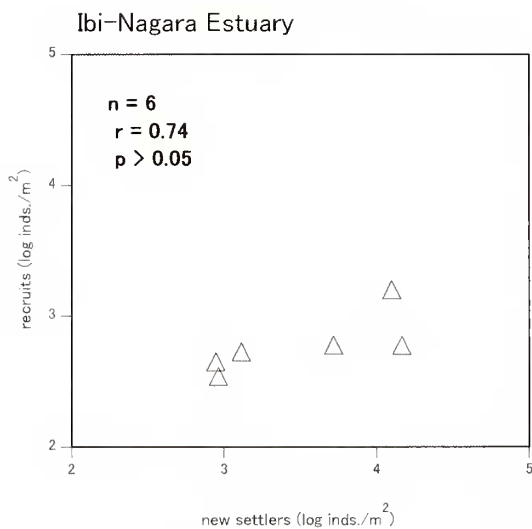
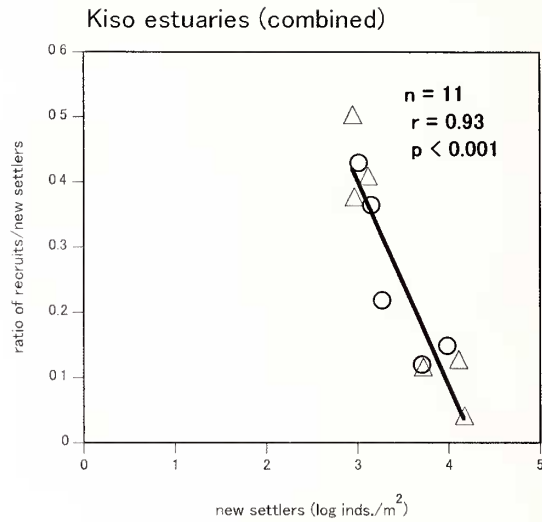
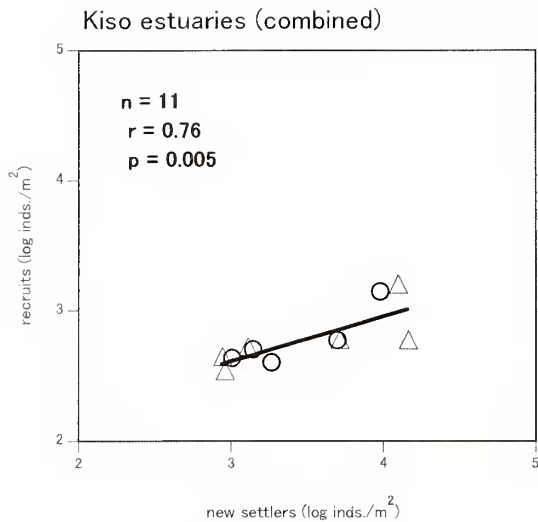


Figure 5. Relationships between densities of new settlers and recruits of *Corbicula japonica* in the Kiso estuaries, central Japan. Upper figures, data for the two estuaries combined; middle figures, data for the Ibi-Nagara Estuary; lower figures, data for the Kiso Estuary; left figures, density of new settlers vs. density of recruits; right figures, density of new settlers vs. the ratio of their densities (recruits/new settlers); open circles, data for the Ibi-Nagara Estuary; triangles, data for the Kiso Estuary; n=number of cohorts.

Based on the data for successful cohorts in the Kiso estuaries, it took nearly two years from larval settlement for individuals to reach commercially viable shell lengths. Takada *et al.* (2001) and Oshima *et al.* (2004) estimated shell growth of clams using growth rings on the shell surface and found a similar growth rate as in the present study.

As indicated in Figs. 3B and 4B, the densities of new settlers in the cohorts identified in 2003, which originated in planktonic larvae and new settlers with much lower densities, were considerably lower than in the other years (Figs. 2B, 2C). Density peaks of new settlers appeared to generate

successful cohorts of benthic stages (compare Fig. 4B with Fig. 4A). However, as indicated by comparing Fig. 3B with Fig. 3A, peaks of densities of planktonic larvae did not always contribute to the generation of successful cohorts of benthic stages. The larvae from earlier and later periods of spawning of the clam every year may not contribute to generating cohorts of new settlers.

Relationships between densities of new settlers and recruits of *Corbicula japonica*

Based on the data from 11 successful cohorts (6 from

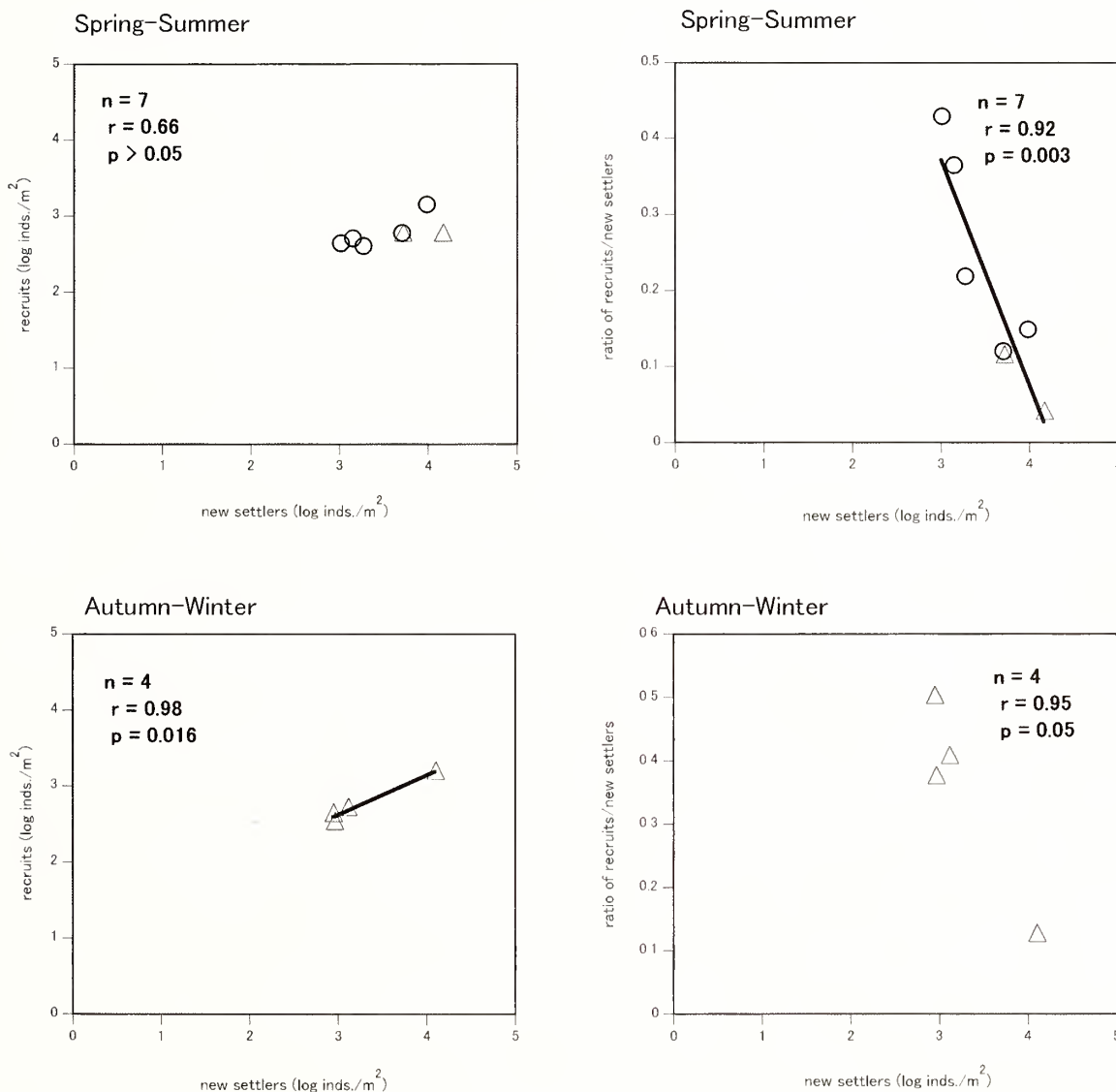


Figure 6. Relationships between densities of new settlers and recruits of *Corbicula japonica* in the Kiso estuaries, central Japan. Upper figures, data for spring-summer cohorts; lower figures, data for autumn-winter cohorts; open circles, data for the Ibi-Nagara Estuary; triangles, data for the Kiso Estuary; n=the number of cohorts.

the Ibi-Nagara Estuary, 5 from the Kiso Estuary), there was a significantly positive correlation between densities of new settlers and recruits in the combined estuaries, but not in each estuary (Fig. 5). There was a significant negative correlation between the density of new settlers and the ratio of their densities (recruits/new settlers) for these estuaries combined and also for each estuary individually (Fig. 5).

The 11 successful cohorts that were divided into two groups, 7 spring-summer cohorts and 4 autumn-winter ones, according to the months with successful recruitment. There was no significant correlation between densities of new settlers and recruits for spring-summer cohorts, whereas there was a significant negative correlation between the density of new settlers and the ratio of their densities (recruits/new settlers) (Fig. 6). The reverse was true for autumn-winter cohorts (Fig. 6): There was a significant positive correlation between densities of new settlers and recruits

for autumn-winter cohorts, but there was no significant correlation between the density of new settlers and the ratio of their densities (recruits/new settlers).

Ontogenetic habitat shift of *Corbicula japonica*

Of the cohorts identified in the Ibi-Nagara Estuary, 4 cohorts (i-iv) were successful in reaching shell lengths (12.0 mm) of commercially important individuals (Fig. 3B). Each cohort had a similar spatio-temporal distribution (Fig. 7): new settlers and small individuals were collected mainly in the upper region of the estuary, large and commercially important individuals were found primarily in the central region. Nanbu *et al.* (2005) found an ontogenetic habitat shift during the benthic stages (from new settlers to commercially important individuals) in mixed cohorts of this clam. An ontogenetic habitat shift was also detected within the same cohort, as indicated in Fig. 7. However, this was not true for

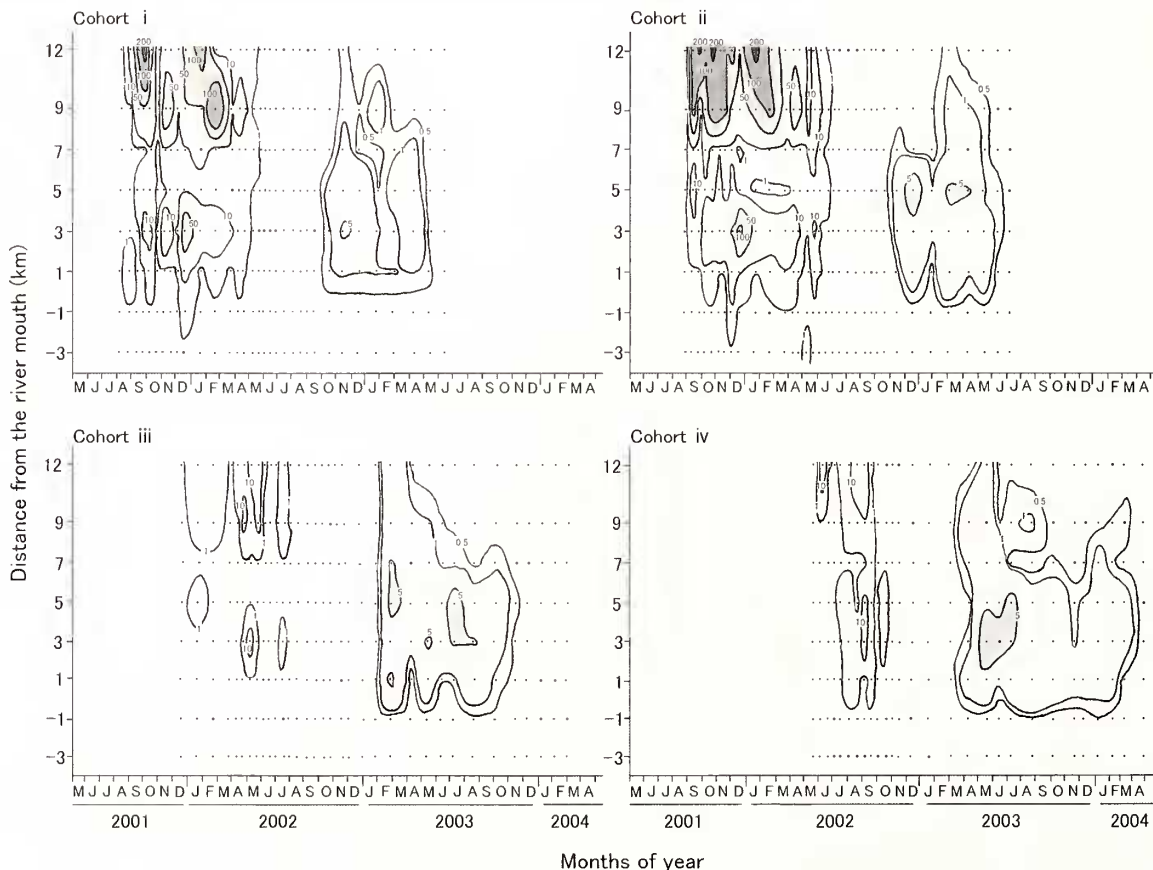


Figure 7. Habitats of different cohorts of *Corbicula japonica* in the Ibi-Nagara Estuary, central Japan. Dots, sampling day/location; solid lines, isopleths of densities of new settlers/small individuals or large/commercial individuals; numerals, density in inds./0.01m²; gray to black areas, the highest density areas with 50 inds./0.01m² or more for new settlers/small individuals and 5 inds./0.01m² or more for large individuals. Left and right isopleths in each figure indicate isopleths for new settlers/small individuals and large/commercial individuals, respectively. Open space between isopleths of new settlers/small individuals and large/commercial individuals in each figure is due to the transition between these two groups, as indicated in Figures 3 and 4.

cohorts in the Kiso Estuary. In the Kiso Estuary, 4 cohorts (1-4) were successful in reaching shell lengths of commercially important individuals (Fig. 4B). All cohorts had similar spatio-temporal distributions (Fig. 8): Benthic stages were collected primarily in the upper region of the estuary.

DISCUSSION

As summarized for densities of different life stages of *Corbicula japonica* in Table 1, there was no significant difference in larval densities between the Ibi-Nagara and the Kiso Estuaries through the three-year investigation. This was also true for new settlers (except for 2003) and for large and commercially important individuals (except for 2001). On the other hand, there were significant differences in the den-

sity of small individuals between the two estuaries: A higher density was detected in the Ibi-Nagara Estuary than in the Kiso Estuary. Because the local fishermen's union (e.g., Akasuka) gets higher annual catch yields of the clam in the Ibi-Nagara Estuary, putting higher fishing pressure on commercially important individuals in the estuary (Mizuno *et al.* 2005), commercially important individuals may in fact have a much higher density in the Ibi-Nagara Estuary. In each estuary, the density of commercially important individuals was significantly higher in 2002, but there was not a significant difference in the densities of larvae and new settlers between sampling years (Table 1). This suggests that processes affecting benthic stages (new settlers and small individuals), not processes affecting larval settlement and larval supply, may contribute to generating the differences in densities of small individuals between these estuaries. However,

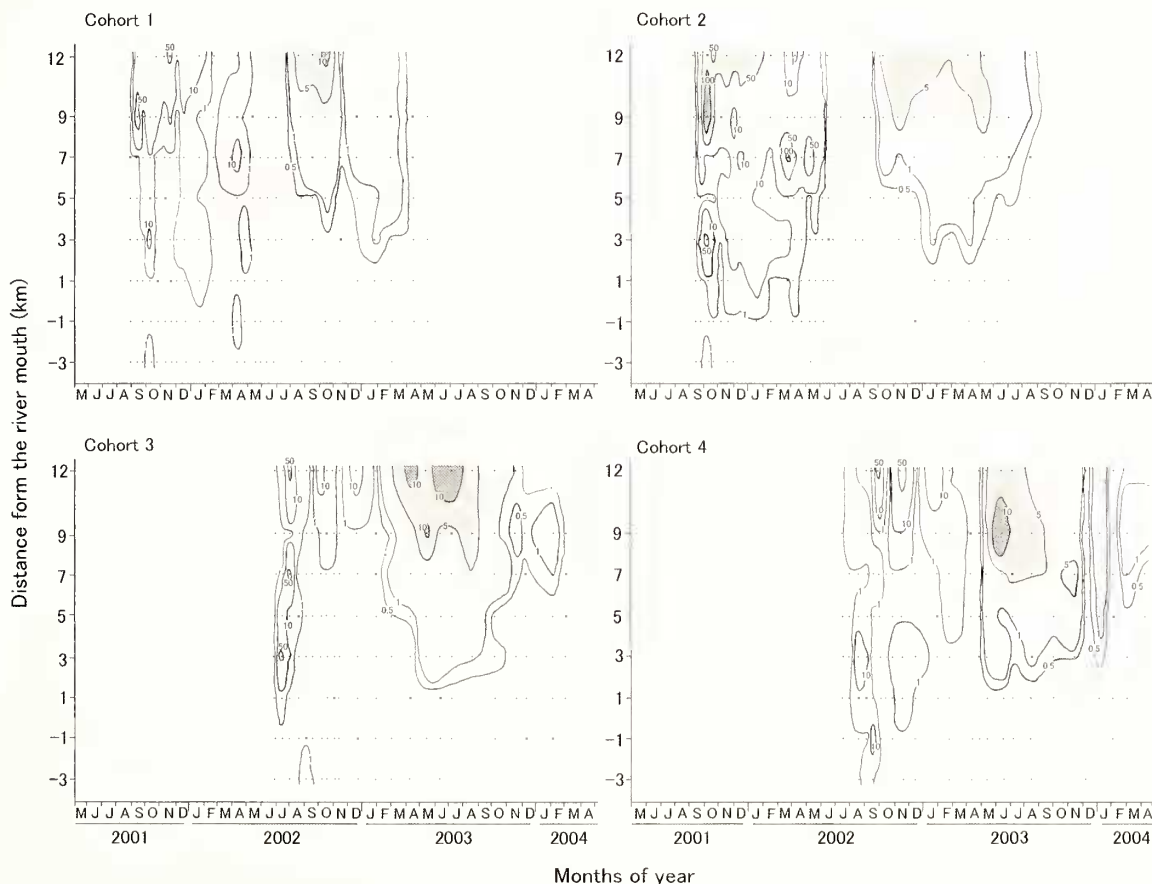


Figure 8. Habitats of different cohorts of *Corbicula japonica* in the Kiso Estuary, central Japan. Dots, sampling day/location; solid lines, isopleths of densities of new settlers/small individuals or large/commercial individuals; numerals, density in inds./0.01m²; gray to black areas, the highest density areas with 50 inds./0.01m² or more for new settlers/small individuals and 5 inds./0.01m² or more for large individuals. Left and right isopleths in each figure indicate isopleths for new settlers/small individuals and large/commercial individuals, respectively. Open space between isopleths of new settlers/small individuals and large/commercial individuals in each figure is due to the transition between these two groups, as indicated in Figures 3 and 4.

the difference in densities of small individuals between the estuaries may not contribute to generating the differences in the densities of the successive benthic stages (large and commercially important individuals) between the estuaries.

For populations of *Corbicula japonica* in the Kiso estuaries, there were significant correlations between the density of new settlers and the ratio of their densities (recruits/new settlers) for each estuary and also for the two estuaries combined (Figs. 5-6). The density of new settlers may have a great influence on the density of recruits. This was also true for spring-summer cohorts, but not for autumn-winter cohorts. According to Mizuno *et al.* (2005), annual catch yields of *C. japonica* in the Kiso estuaries are sustained by individuals (new cohorts) reaching commercially viable shell lengths (12.0 mm) of large individuals in spring to summer every year. Densities of these new cohorts drastically decrease in winter due to high mortality caused by fishing pressure, so that density-dependent processes may not operate on autumn-winter cohorts. On the other hand, density-dependent processes may affect spring-summer cohorts because higher densities of new settlers and small individuals were observed in summer to autumn every year. We conclude that densities of large and commercially important individuals were determined by benthic processes, not by larval supply.

It is not immediately apparent why the shift in an ontogenetic habitat of *Corbicula japonica* was detected only in the Ibi-Nagara Estuary. Nanbu *et al.* (2005) also reported the occurrence of a similar ontogenetic habitat shift for mixed cohorts in the Ibi-Nagara Estuary. They proposed alternative scenarios to explain this shift: (1) The shift may be generated by tidal/diurnal/seasonal/ontogenetic migration using the byssus or other means, as observed in many common bivalves (Hamada and Ino 1954, Sigurdsson *et al.* 1976, Prezant and Chalermwat 1984, Lane *et al.* 1985), particularly in light of the salinity sensitivity of *Corbicula japonica* during ontogeny (Saito *et al.* 2002, Kuwabara and Saito 2003), (2) The shift does not occur within the same cohort; habitats may differ depending on cohort (*i.e.*, the site-specific mortality may differ depending on benthic stage), so that the shift only appears to occur within the same cohort; and (3) The shift does not occur within the same cohort, and the site-specific mortality may differ depending on benthic stage, so that the shift appears to occur within the same cohort. Because of the cohort separation observed in the present study, indicating the occurrence of an ontogenetic habitat shift within the same cohort and because all benthic cohorts had a similar distribution pattern for each estuary, scenario 2 may be rejected. However, we cannot evaluate scenarios 1 or 3 unless we measure the site-specific mortality in the Ibi-Nagara Estuary.

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